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THE EXCHANGE OF MATERIAL BETWEEN NUCLEUS AND CYTOPLASM IN PEPEROMIA SINTENISII[1]

WILLIAM H. BROWN

(WITH PLATE XIII)

In describing the development of the embryo sac of *Peperomia sintenisii*, the writer showed that at the time of the fusion of the sexual nuclei globules of cytoplasm were taken into the fusion nucleus. This phenomenon was not studied in detail at that time, but seemed to be worthy of further study, as it offered the possibility of throwing some light on the relation between cytoplasm and nucleoplasm. For the investigation of this problem material which had been fixed in chromacetic acid was cut 10 μ thick and stained with Flemming's triple or Haidenhain's iron alum-hematoxylin and eosin.

As the male nucleus of *Peperomia sintenisii* approaches the egg, just before fusion, both nuclei come to have cup-shaped depressions in the sides facing each other (*figs. 1–5*); the other parts of the nuclei, however, have a fairly regular shape. The depressions in the two nuclei may correspond closely to each other (*figs. 2, 3*), or they may not (*figs. 1, 5*). The number of depressions is also variable in different nuclei, there being one in each nucleus in *figs. 1, 2*, two in *fig. 3*, while *figs. 4* and *5*, which were taken from the same pair of nuclei, show three depressions in each nucleus. When the two nuclei come together, the nuclear membranes disappear where the nuclei touch each other, but remain intact around the depressions, the cytoplasmic contents of which appear as vesicles within the nucleus (*figs. 6–18*). *Fig. 6* shows a case in which one vesicle is caught in the nucleus while two others are probably in the process of being inclosed. *Fig. 7* shows one vesicle inclosed in the nucleus and another nearly inclosed. The number and size of the vesicles, like the depressions giving rise to them, are variable (*figs. 8–18*). When the cytoplasm is first inclosed in the vesicle, it takes the usual cytoplasmic stains (*figs. 7–9*), but it gradually stains less and less until the vesicles are distinguishable from the clear nuclear sap only by the membranes which surround them. *Figs. 10–18* show various stages in the disappearance of the staining reaction in the cytoplasmic vesicles. In *figs. 10* and *11* there is a trace of stain; in *figs. 12–14* there is no stain in one of the vesicles; while *figs. 15–18* show vesicles the contents of which are indistinguishable from the surrounding clear nuclear sap. Shortly after this stage the membranes around the vesicles begin to break down and disappear (*figs. 19, 20*).

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[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, No. 11.

The phenomenon just described seems to be a constant characteristic of fertilization in *Peperomia sintenisii*, as no fusions were observed in which cytoplasm was not taken into the nucleus, although more than 50 nuclear fusions of this stage were studied. That the phenomenon is not due to shrinkage in fixing is shown by the regular appearance of the other nuclei in the sac, as well as of all parts of the sexual nuclei except the sides facing each other at the time of fusion. This view is confirmed by the further development, when by focusing the vesicles can be seen to be completely inclosed within the nucleus. This is shown in *figs. 12, 13*, and *15*, where one nucleolus is below and the other above the vesicle.

The growth of any nucleus must be at the expense of material obtained from the cytoplasm, and so it is evident that some material must pass from the cytoplasm to the nucleus. The phenomenon just described, where a vesicle of cytoplasm becomes nucleoplasm, seems to show that all of the essential constituents of cytoplasm may be changed into nucleoplasm.

The presence of the cytoplasmic vesicle within the nucleus gives the nucleus a greater surface for the intake of cytoplasm and this may be of advantage to it at this stage.

The membrane around the cytoplasmic vesicle did not disappear, however, before the cytoplasm seemed to be changed to nucleoplasm. This supports LAWSON's conclusion that the nuclear membrane is formed by the cytoplasm coming into contact with the nuclear sap, for the membrane here as in other fusing nuclei disappears, probably by absorption, when nucleoplasm is on both sides of it. LAWSON bases his conclusion on the fact that in the reorganization of nuclei the nuclear membrane appears at the time that the clear nuclear sap appears outside the chromosomes and in contact with the cytoplasm. The same thing appears to be true in the case of *Peperomia sintenisii*

(BROWN '08). It is not necessary to assume that the process is a simple chemical precipitation, because it may be a physiological response.

The question now arises as to what happens when the nuclear membrane disappears during prophase. In *Peperomia sintenisii* the incipient spindle fibers form a dense felt over the nucleus before the membrane disappears. The appearance of spindle fibers before the disappearance of the nuclear membrane has been described in Lilium, Podophyllum, and Helleborus (MOTTIER '97), Equisetum (OSTERHOUT '97), Cobea and Gladiolus (LAWSON '98, '00), Pellia and Anthoceros (DAVIS '99, '01), Lavatera (BYXBEE '09), Osmunda (SMITH '00), Larix (ALLEN '03), and a number of other genera. In *Peperomia sintenisii*, as in a number of other forms, the appearance of the cytoplasm around the nucleus is at this stage quite different from what it was before the appearance of the fibers, and the disappearance of the membrane may be connected with this change of the cytoplasm.

When the cytoplasmic vesicle in *Peperomia sintenisii* becomes nucleoplasm, the question arises as to whether the cytoplasm has passed into the nucleus and nucleoplasm into the vesicle, or whether the cytoplasm is changed while in the vesicle. If, as seems probable, the nuclear membrane is formed by the interaction of the nuclear sap and the cytoplasm or some part of the cytoplasm, it seems evident that that part of the cytoplasm which participates in the formation of the membrane could not pass through the membrane, because, if it did, on coming into contact with the nucleoplasm it would only thicken the membrane. This does not mean, however, that no substances can pass from the nucleus to the cytoplasm or from the cytoplasm to the nucleus. It seems evident, however, that in *Peperomia sintenisii* the cytoplasmic vesicle, on account of its position, is converted into nucleoplasm through the activity of the nucleus, for there is no more reason for thinking that this part of the cytoplasm would change itself than there is for thinking that all of the cytoplasm would do the same thing. Then since the cytoplasm cannot pass unchanged into the nucleus, it is probable that some substance passes out into the cytoplasm and changes the cytoplasm in such a way that it may then be taken into the nucleus. It is not likely that this method of exchange is confined to this particular case, but since all of the essential constituents of protoplasm go into the nucleus of *Peperomia sintenisii*, it seems probable that the same thing happens in other organisms, and that this is rendered possible, as is probably the case in *P. sintenisii*, by the action of some substance or substances which continually pass out of the nucleus and cause a change in the cytoplasm.

It may be that the previously mentioned change of the cytoplasm around the nucleus, just before division, is connected with the accumulation, outside the nucleus, of the substance which has passed from the nucleus; and that the disappearance of the nuclear membrane is connected with a change of the cytoplasm causing a suspension of the reaction between the cytoplasm and nucleoplasm. The disappearance of the membrane might then be by absorption, analogous to the absorption of the nuclear membrane between two fusing nuclei. The substances which made possible this absorption, by accumulating outside the nucleus, would probably not be the same as those which, by reacting with the cytoplasm, caused the formation of the nuclear membrane. On the other hand, it seems not improbable that during division the nuclear sap loses its power of reacting with the cytoplasm, for it may become mixed with the cytoplasm or form a definite part of the cytoplasm, as in the maturation of certain animal eggs.

At the division of a cell of *Peperomia sintenisii*, as in other plants, the nuclear sap and nucleolus are lost in the cytoplasm; and so it is evident that nucleoplasm may also become a part of the cytoplasm. In many animals the clear substance which passes from the nucleus at maturation goes to form a special part of the embryo, and the passing of nucleoplasm to the cytoplasm has been considered as a method by which the chromosomes influence the development and activities of an organism. The observations on *Peperomia sintenisii* seem to show that some substance or substances are being constantly passed from the nucleus to the cytoplasm, and this may also be a means by which the nucleus controls the activities of the cell. The control of the cytoplasm by the "resting" nucleus seems to be well illustrated in the formation of the blepharoplast of Derbesia (DAVIS **'08**). Here radiations pass from the nucleus out to the cell wall, and at the ends of these radiations granules which fuse to form the blepharoplast are laid down.

Summary

At fertilization in *Peperomia sintenisii* globules of cytoplasm surrounded by a nuclear membrane are inclosed in the fusion nucleus. The cytoplasm globule gradually assumes the appearance of nuclear sap, after which the membrane around it disappears.

This phenomenon seems to show that all of the essential constituents of cytoplasm can be changed to nucleoplasm.

The appearance of a nuclear membrane when cytoplasm and nuclear sap meet, and the absorption of the membrane when nucleoplasm is on both sides of it, seem to show that the nuclear membrane is formed by the interaction of cytoplasm and nuclear sap.

If the membrane is formed in the above manner, it is probable that the contents of the cytoplasmic vesicle could not be changed to nucleoplasm by a gradual exchange of material between the nucleus and cytoplasm, for all of the constituents of the cytoplasm could not pass through the membrane, because some would react with the nucleoplasm and thicken the membrane. Since, however, the cytoplasmic contents of the vesicle are changed, this change is probably due to some substance which has come from the nucleus.

It is probable then that cytoplasm before being taken into a nucleus is changed by some substance which has passed from the nucleus, because it is not likely that *Peperomia sintenisii* differs from other organisms in such a fundamental activity of protoplasm.

The passage of substance from the nucleus is probably continual and may be a means by which the "resting" nucleus controls the cytoplasm.

The material, which made these observations possible, was collected in Jamaica by Professor D. S. JOHNSON, to whom the writer is greatly indebted.

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EXPLANATION OF PLATE XIII

All drawings were made with the aid of a camera lucida, using a No. 8 ocular and a 1.5^{mm} objective.

Fig. 1.—Male and female nuclei of *Peperomia sintenisii* approaching each other; each nucleus shows one depression in side facing the other.

Fig. 2.—Later stage of same.

Fig. 3.—Male and female nuclei in contact; each shows two depressions.

Figs. 4, 5.—Two sections through same pair of nuclei, each of which contains three depressions.

Fig. 6.—Early stage of fusion; nuclear membrane has disappeared where nuclei have come into contact with each other, causing the entire inclosure of one and partial inclosure of two other cytoplasmic globules.

Fig. 7.—About same stage as *fig. 6;* one globule entirely, another partially inclosed.

Fig. 8.—Fusion nucleus containing one vesicle of cytoplasm surrounded by a nuclear membrane.

Fig. 9.—Fusion nucleus containing two vesicles of cytoplasm.

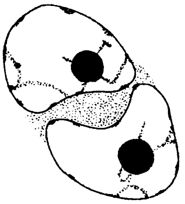
Figs. 10, 11.—Later stages; the cytoplasm stains less densely.

Figs. 12–14.—Still later stage; the staining reaction of cytoplasm has completely disappeared from one of the vesicles.

Figs. 15–18.—The contents of the vesicles are indistinguishable from the surrounding clear nuclear sap.

Fig. 19.—The membrane around the vesicle is beginning to disappear.

Fig. 20.—Later stage in the disappearance of the membrane around the vesicle.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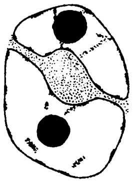
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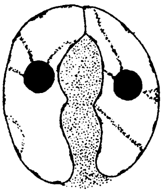
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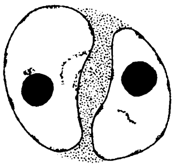
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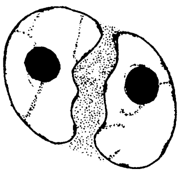
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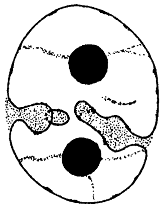
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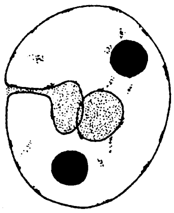
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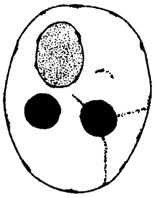
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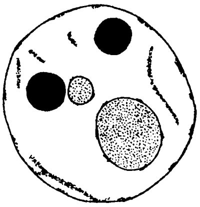
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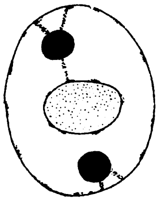
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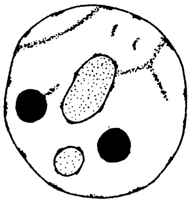
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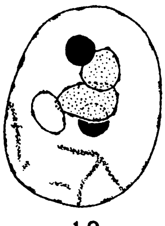
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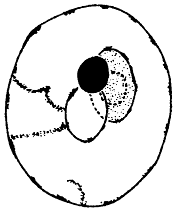
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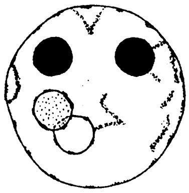
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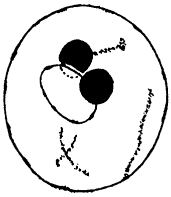
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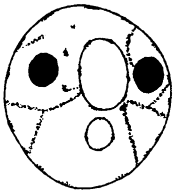
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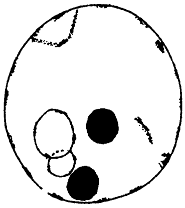
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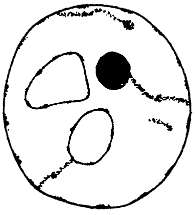
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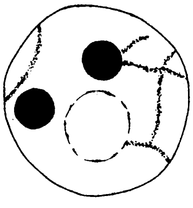
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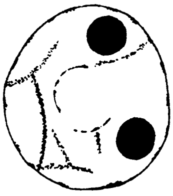
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BROWN on PEPEROMIA